# A SYSTEMATIC AND BIOGEOGRAPHIC REVIEW OF *RAILLARDIOPSIS* [*RAILLARDELLA*] *MUIRII* (ASTERACEAE: MADIINAE), WITH SPECIAL REFERENCE TO A DISJUNCT CALIFORNIA COAST RANGE POPULATION

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## Abstract

Morphological, cytological, and controlled growth chamber studies demonstrate that a widely disjunct *Raillardiopsis* population in the Santa Lucia Range of central coastal California is conspecific with *R.* [*Raillardella*] *muirii* of the southern Sierra Nevada. Morphological and cytological variation detected within Sierran *R. muirii* essentially encompasses that of the Santa Lucia Range population. A revised description of this little understood species and a key to the two species comprising the genus are presented. Biological and geological considerations bearing on the origin of the Santa Lucia Range disjunction are discussed. High dispersibility, paleoecological factors, and plate tectonics have potentially contributed to this seemingly enigmatic species distribution.

The isolated occurrence of a *Raillardiopsis* population on Ventana Double Cone in the Santa Lucia Mountains of central coastal California has been regarded ". . . a phyto-geographic occurrence of first magnitude in California floristics" (Howitt and Howell 1973). This population indeed raises interesting questions about the evolutionary history of *Raillardiopsis,* a little-known genus resurrected from within *Raillardella* based on morphological, cytological, and chloroplast DNA evidence (Baldwin 1989). The two rare species comprising *Raillardiopsis* have ranges far removed from the Santa Lucia Mountains. *Raillardiopsis scabrida* (Eastw.) Rydb. is restricted to high peaks and ridges in the inner North Coast Ranges of California from Lake to Trinity counties, with two Southern Cascade outliers in Shasta County. *Raillardiopsis muirii* (A. Gray) Rydb. (Figs. 1 and 2) has long been considered a southern Sierra Nevada endemic. In a group of rare perennials a disjunction of the magnitude represented by the Santa Lucia Range population could have important systematic or biogeographic implications.

Though the existence of the Ventana Double Cone population has been known since 1962, when it was discovered by Clare Hardham (Griffin 1975), the specific identity of these plants has remained ambiguous. This is largely attributable to lack of specimens from this remote locality and inadequate published descriptions of *Raillardiopsis* species. The earliest reference to the Santa Lucia plants

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Madroño, Vol. 37, No. 1, pp. 43–54, 1990

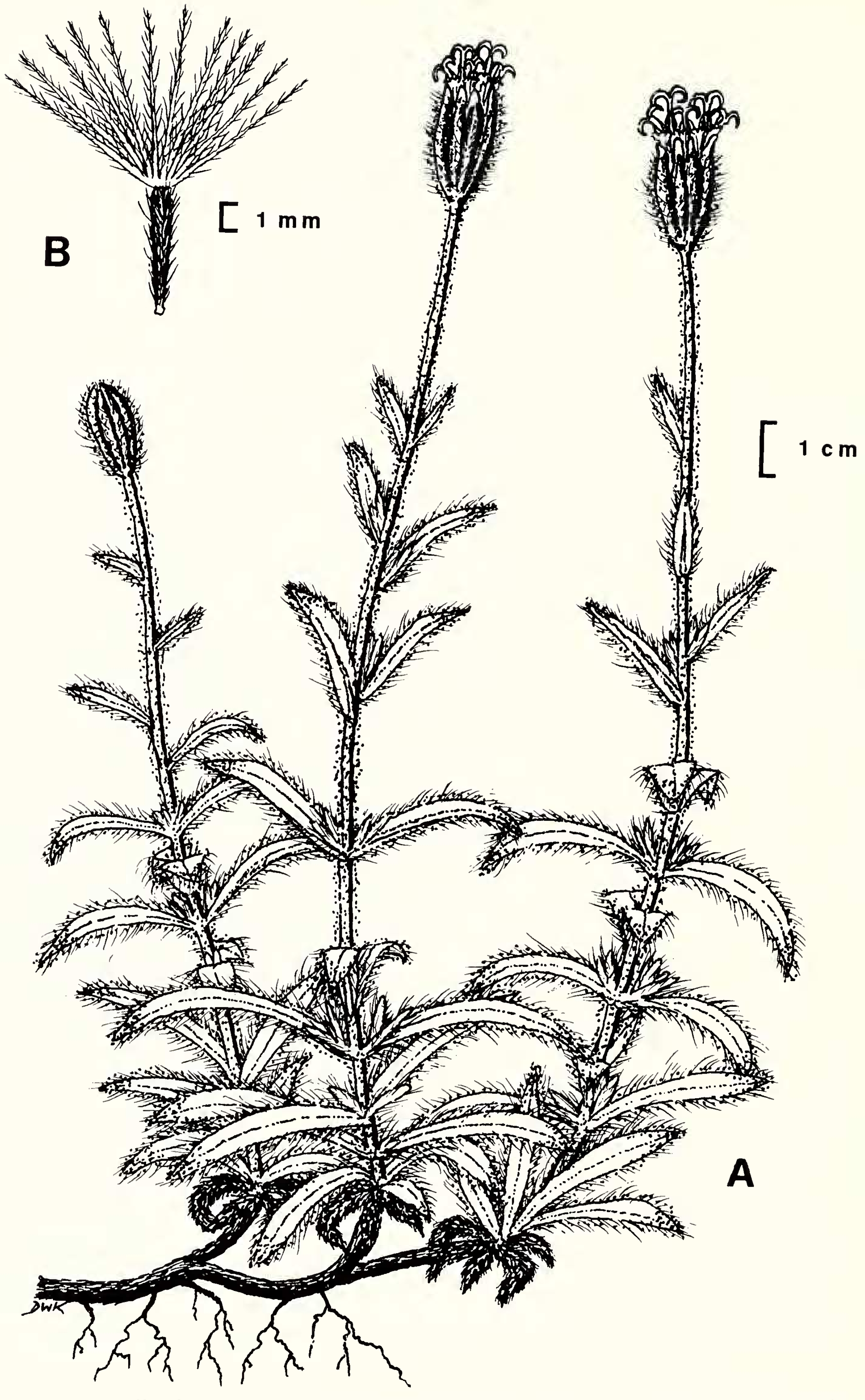

FIG. 1. *Raillardiopsis muirii* (A. Gray) Rydb. A. Habit. B. Mature achene with pappus.

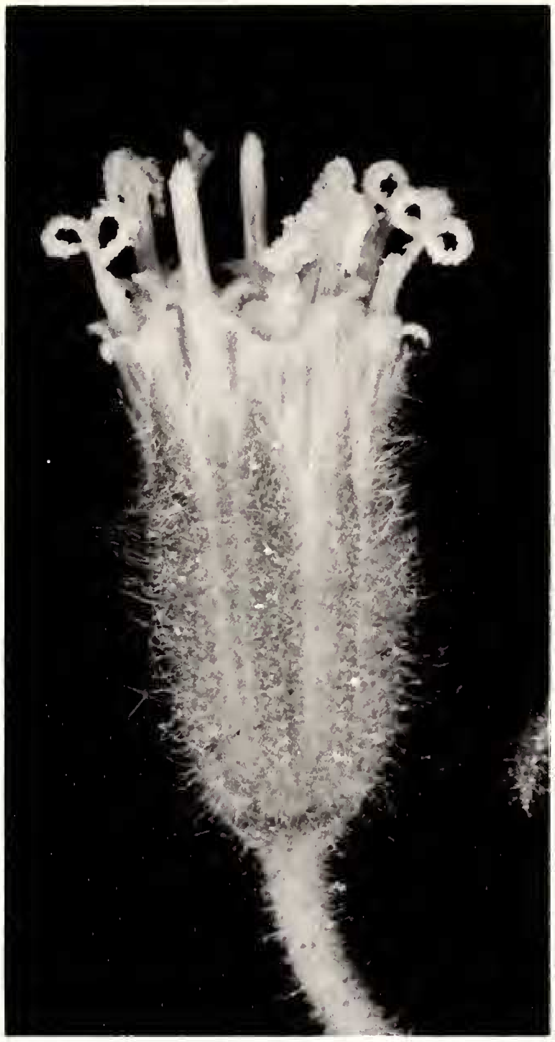

FIG. 2. Capitulum of *Raillardiopsis muirii*. Note the distinctive spreading trichomes on the abaxial bract surfaces.

as *Raillardiopsis* (Howitt and Howell 1973) immediately followed the first known collection made in 1972 [*Steven Talley s.n.* (DAV)]. Further study by J. R. Griffin revealed that the Ventana plants shared closest relationship, and were perhaps conspecific, with *R. muirii*. Griffin (1975) concluded, "if the Ventana population is *R. muirii*, this plant is one of the most restricted and most interesting montane disjuncts in the Santa Lucias; if it is a new species, it is probably the most restricted endemic above 1200 m". Unfortunately, further work was hindered following the Marble Cone Fire of 1977 because of trail closure and shrub overgrowth.

This study was undertaken to assess the evolutionary and biogeographic relationships of the Santa Lucia Range (hereafter "Ventana") *Raillardiopsis* to *R. muirii*. Morphological, cytological, and reproductive characteristics of these plants were investigated. An improved description of *R. muirii* and a key differentiating this species from the similar *R. scabrida* were prepared to prevent future confusion concerning the limits of these taxa.

## FIELD OBSERVATIONS

The first author visited Ventana Double Cone in July of 1986 and found a vigorous *Raillardiopsis* population on the steep western slope. The plants were scattered mats in decomposing granitic scree and bedrock crevices with little other vegetative cover. A few small plants were previously observed on and immediately east of the summit in 1975 and 1981 (V. Yadon oral comm.). The similar granitic slopes of "Ventana"—the notched ridge north of Ventana Double Cone—and on Ventana Cone may support additional *Raillardiopsis* populations.

## METHODS

Vouchers, floral buds, and achenes were field-collected. Buds were fixed in Carnoy's (6 ethanol : 3 chloroform : 1 glacial acetic acid; v:v:v) or modified Carnoy's (6 chloroform : 3 ethanol : 1 glacial acetic acid) solutions. Chromosome counts and meiotic associations were determined at meiotic metaphase I in acetocarmine. Pollen fertility was estimated from percent stainability with cotton blue in lactophenol. Fourteen Ventana [*Baldwin 618* (DAV)], six *R. muirii* [*Baldwin 683* (DAV)], three $F_1$ *B618* (seed) × *B683* (pollen), and nine $F_1$ *B683* (seed) × *B618* (pollen) plants were grown from seedlings under uniform growth chamber conditions (21°C, 16 hour light; 11°C, 8 hour dark) in U.C. potting mix or with ca. equal amounts of coarse pumice. Artificial hybridizations were performed by rubbing pollen-shedding capitula together. These hybridizations involved the same Ventana parent but different *R. muirii* individuals. Embryos were excised and germinated under continuous light. Parental embryos were germinated on wet filter paper. After surface-sterilization (10% bleach, 20 min), $F_1$ embryos were excised and germinated on Murishige minimal organics media (GIBCO 510-3118) + 2% sucrose. Self-incompatibility of Ventana *Raillardiopsis* was assessed by identifying all progeny from interspecific crosses with species other than *R. muirii* serving as staminate parents. Additionally, fruit set in all unmanipulated heads was monitored. Herbarium specimens at CAS, CHSC, DAV, GH, JEPS, PGM, RSA, THRI, and UC were examined. These represented 12 of the 18 known populations of *R. muirii,* several populations of *R. scabrida,* and all known collections of Ventana *Raillardiopsis* (see Baldwin 1989).

## RESULTS AND DISCUSSION

*Morphological comparisons.* The range of morphological variation detected in *R. muirii* essentially encompassed that found in the Ventana population. The only exceptions were slightly greater leaf crisping, leaf deflexion, and leaf width among some Ventana individuals relative to any *R. muirii* examined. These differences persisted under growth chamber conditions in individuals grown from seedlings. *Raillardiopsis muirii* displayed no crisping under these conditions, though this character was observed to a minor degree in field material. Artificial hybridization between Ventana and *R. muirii* individuals also indicated a genetic basis for leaf crisping in Ventana plants. All but two individuals of the $F_1$ generation displayed noticeable leaf crisping, regardless of the population serving as seed parent. All other (interspecific) combinations involving Ventana *Raillardiopsis* (Baldwin 1989) have yielded $F_1$ individuals with evident leaf crisping.

*Cytology.* Chromosome counts of all *R. muirii* (*B615, B653, B683*) and Ventana *Raillardiopsis* (*B618*) revealed eight bivalents at meiotic metaphase I. The single report of $n=16$ for *R. muirii* (Powell and Powell 1978) is a miscommunication of a somatic count ($2n=16$) by Kyhos et al. (Carlquist 1959). Pollen stainabilities of single Ventana (99%; *B618*) and *R. muirii* (84%; *B683*) plants indicated normal fertility. Meiotic analyses of the *R. muirii* × Ventana $F_1$ generation revealed a modal configuration of six bivalents and a ring of four in five individuals, and consistently eight bivalents in three plants. Unambiguous hybrid morphology (leaf crisping) in one of the latter three plants, of Sierran seed-parentage, strongly suggests chromosomal structural heterozygosity in the parental *R. muirii* population, i.e., one genome being shared with the Ventana population, the other differing by a single reciprocal translocation. Pollen fertility ranged from 35% to 50% ($\bar{x}$ = 43.6%) in the structurally heterozygous $F_1$ plants and from 56% to 66% ($\bar{x}$ = 60.3%) in the structurally uniform $F_1$ individuals. *Raillardiopsis muirii* × Ventana hybrids were easily produced in both directions. The chromosomal divergence detected within *R. muirii* is minor compared to that found between *R. muirii* and *R. scabrida* (Baldwin 1989). All chromosome counts of *R. scabrida* [*Baldwin 620* (DAV), *Baldwin 676* (DAV), *Taylor et al. 9089* (DAV, RSA)] have revealed $n=7$, in agreement with counts by Strother (1983).

*Breeding system.* Ventana *Raillardiopsis* is strongly self-incompatible. Reportedly, interspecific crosses in Madiinae can elicit selfing in otherwise self-incompatible species (Clausen et al. 1945). All but one progeny from 104 Ventana *Raillardiopsis* heads utilized as pistillate parents in crosses with Madiinae other than *R. muirii* were, however, hybrid or inviable. The single plant resulting from selfing was unusually robust and morphologically distinctive, with corolla, bract, and habit aberrations. No unmanipulated heads bore fruit.

*Taxonomic conclusions.* Comparative evidence indicates that the Ventana *Raillardiopsis* population belongs within *R. muirii.* We hesitate to segregate the Ventana element as a subspecies given its lack of sharp morphological distinction from all Sierran populations. Subspecific recognition of these plants would require reliance on small modal differences as diagnostic morphological characters, not allowing definite identification of specimens from unknown localities. Apparent morphological variation among Sierran populations indicates that such treatment would necessitate further dissection of the species into taxa of questionable phylogenetic significance.

*Revised description.* Confusion about the identity of the Ventana population was, in part, attributable to descriptions of *R. muirii* from few and fragmentary herbarium records. This situation has improved, largely owing to J. T. Howell (see Howell 1961), L. Norris, and J. Shevock, who extensively collected *R. muirii* in the southern Sierra Nevada. The following description and key to *Raillardiopsis* are provided to clarify *R. muirii* and to allow identification of any populations that may await discovery.

**Raillardiopsis muirii** (A. Gray) Rydb., North American Flora 34: 318–320. 1927 (Fig. 1).—*Raillardella muirii* A. Gray, Bot. Calif. 1:618. 1876.—Type: USA, California, Sierra Nevada, "the station unknown", *J. Muir s.n.* (holotype, GH!; isotype; CAS!). According to a letter accompanying the holotype from John H. Redfield to Asa Gray (28 Feb 1876), the type specimen was ". . . in a small collection sent . . . by John Muir—from the Sierras in vicinity of Yosemite". No other collection information was given. The most northerly populations known are in the Kings River drainage. Muir's earliest explorations of the Kings River region occurred in 1873 and 1875, including the North Fork of the Kings River vicinity and the "yosemite of the Middle Fork of the King's River"—Tehipite Valley (Muir 1938, 1977). These two areas possess the largest and most extensive known *R. muirii* populations (CNDDB 1989). The species was rediscovered by Alice Eastwood in 1905 at Tehipite Valley (Eastwood 1907).

Clumped to mat-forming herbaceous perennial with spreading, often extensively branched, woody rhizomes, to at least 1.5 cm diam. Aerial stems several to many, crowded, the short, densely-leaved vegetative shoots and dead growth often forming carpets extending to at least 2.25 m. Flowering stems erect to ascending, leafy throughout, 7–54 cm high, simple to several branched, generally from above middle, greenish-yellow to dark purplish, white-hirsute to villous and sparingly glandular below, the hispidulous, spherical to tack-shaped gland-tipped hairs becoming predominant above. Leaves green to gray-green, sessile, linear to narrowly lanceolate, entire, flat to strongly crisped-coiled, ascending to apically or basally deflexed, 9–42 mm long, (1–)2–5(–6) mm wide, to smaller at extreme base of stem and above lowest branches or axillary shoots, opposite at base to above middle, alternate above, irregularly white-hirsute to villous and glandular; glands like those on stems, most conspicuous on leaf apices and upper leaves; leaf apices abruptly to narrowly acute; leaf margins slightly revolute. Heads terminating stems and branches, discoid, (elliptic-) narrowly to broadly campanulate or turbinate; capitular bracts green to purple, 8–13 mm high, (5–)7–16, uniseriate, subequal, mostly half-enveloping single florets with fewer, nearly paleaceous bracts between these, basal margins largely coalescent at anthesis, to mostly free and spreading at fruiting maturity, white-hirsute to villous and conspicuously glandular abaxially and on inner apex, with prominent, stramineous, essentially glabrous adaxial midrib; florets 7–29, all functionally bisexual; corollas yellow, 6.5–10 mm long, tubular, constricted basally; anthers yellow; stylar branches hispidulous. Achenes black, 4–7.5 mm long, 0.5–1.2 mm wide, terete, linear, straight to slightly curved at acute base, densely white ascending-hirsute; pappus bristles flattened, ciliate-plumose to tip, purplish-white to tawny, 9–17, 5–11 mm maximum length. Chromosome number $n=8$.

Under growth chamber conditions certain characters exceeded the above. Main stem leaves of one Ventana individual became very robust, to 9 mm wide. Unusually extensive branching of most plants was also observed.

## KEY TO SPECIES OF *RAILLARDIOPSIS*

A. Heads strictly discoid; bracts hirsute to villous and glandular abaxially; achenes 4–7.5 mm long, 0.5–1.2 mm wide; pappus length equal to or longer than achene; leaves green to grayish-green, markedly acute, not auriculate-clasping on upper stem. .................................................... *R. muirii*

A′ Heads with 0–3 rays; bracts glandular abaxially with villous apical margins; achenes 5–9 mm long, 1.3–2.4 mm wide; pappus length equal to or shorter than achene; leaves blue-green to grayish blue-green, acute to obtuse, often auriculate-clasping on upper stem. ............................................ *R. scabrida*

Heads of live, rayless *R. scabrida* often appear distinctly elliptic in silhouette, or constricted at summit of bracts, to a much greater extent than those of *R. muirii.* This character is obscured in pressed material.

*Distribution and ecology. Raillardiopsis muirii* is a California endemic known from ca. 19 populations (Fig. 3) on granitic exposures or granitic-derived soils in mixed conifer forest and chaparral openings, mountain slopes, ridges, and valley bottoms from 1190 to 2500 m elevation in the southern Sierra Nevada from Fresno to Kern counties and on Ventana Double Cone, Santa Lucia Range, Monterey County (CNDDB 1989). With the exception of three southern outliers (Baker Point, Church Dome, Owens Peak), the Sierra Nevada populations are confined to the drainages of the Kings River and Kaweah River. Flowering has been reported from early June to

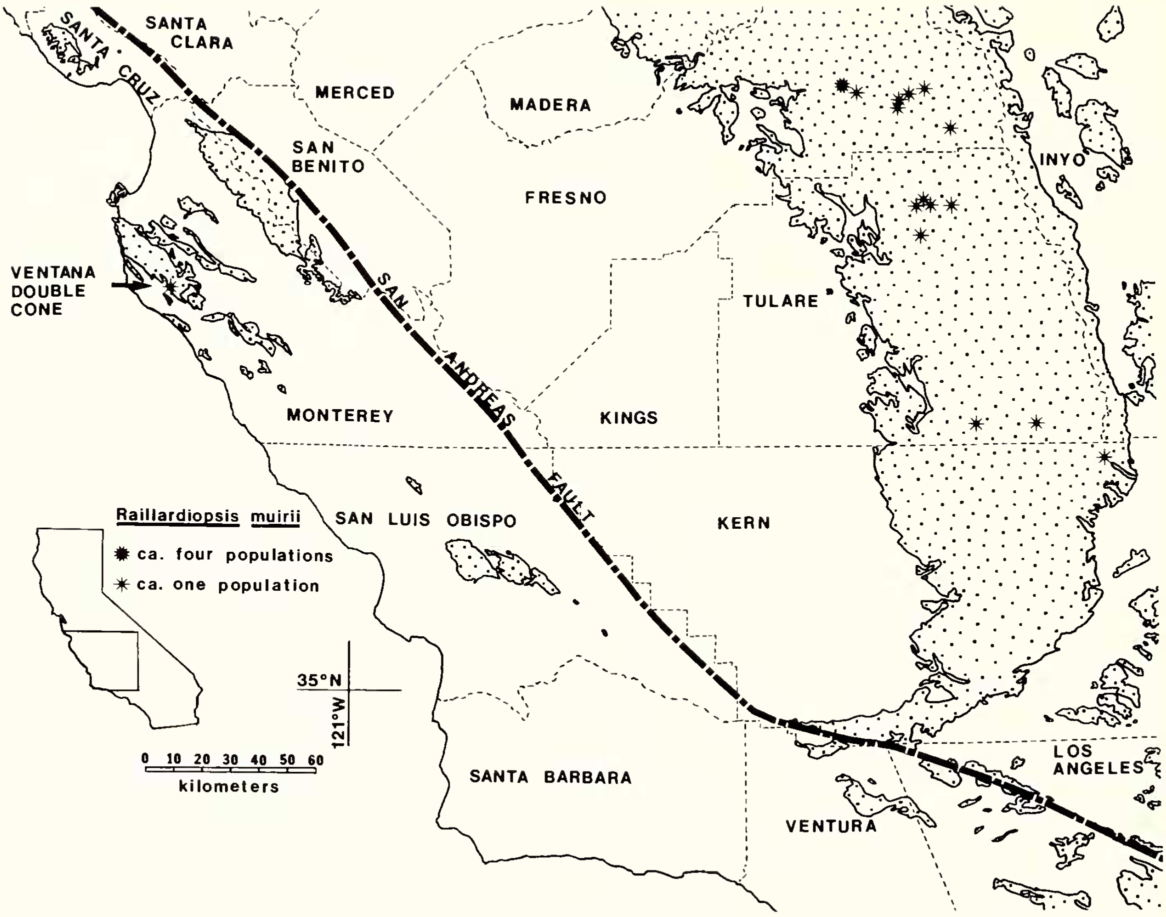

FIG. 3. Natural distribution of *Raillardiopsis muirii* and granitic exposures (stippled areas) in central California. Extensive non-granitics within the Sierran batholith are not shown.

early October, one collection nearing anthesis in mid-May. Several populations are reported to comprise fewer than 100 individuals (CNDDB 1989). The species is listed as "rare and endangered" by the California Native Plant Society (Smith and Berg 1988) and as a "sensitive" species by the U.S. Forest Service (J. Shevock pers. comm.).

*Biogeographic history.* The major range disjunction between Sierran and Ventana *R. muirii* populations is remarkable in light of their apparent restriction to granitic substrates (Fig. 3). Granitic exposures in the South Coast Ranges of California are limited and widely separated because of extensive blanketing of the Salinian pluton basement by late Cretaceous and Cenozoic sediments (Page 1966, 1981, 1989; Compton 1966). The youngest significant overlying sediments reported to contact basement are Miocene, when the Santa Lucia Range was submarine (Raven and Axelrod 1978). Given the Oligocene age of the oldest Compositae fossil evidence (Muller 1981), it appears that granitic exposure in the South Coast Ranges has not exceeded its present extent within the history of *R. muirii.*

*Raillardiopsis muirii* may have had a wider ecological amplitude in the past. The species has no mineralogical requirement for granitic soils, based on successful cultivation in non-granitic mixes. Mortality from root necrosis and microbial infection was, however, encountered and may be a significant factor in the field. Present occurrence in sites with little plant cover may reflect secondary restriction to habitats with reduced competitive interference, as proposed for "paleoendemic" or ecotype "depleted" taxa (Stebbins 1942; Raven and Axelrod 1978). *Raillardiopsis scabrida* occurs in similarly semibarren sites on Franciscan metamorphic substrates. The patchy distribution of both species and their large geographic separation from one another suggest more extensive past occurrence. Fossil evidence demonstrates that many narrowly-endemic taxa in California were once considerably more widespread (Raven and Axelrod 1978).

The presence of relict *Abies bracteata* in the Santa Lucia Range indicates that these mountains have served as a refugium. This species, known from fossil Miocene floras in western Nevada (Axelrod 1976), is today restricted to the Santa Lucia Range, including Ventana Double Cone. Axelrod suggested that *A. bracteata* probably occurred in the Sierra Nevada during the Pliocene, and perhaps in the more southerly Coast Ranges, until the Xerothermic Period of the Quaternary, but was eliminated in both regions by the drier, warmer climate. These xerothermic conditions would likely have had similar impact on any populations of *R. muirii* bridging the Santa Lucia Range and southern Sierra Nevada.

Modern associates of both Sierran and Ventana *R. muirii* offer little to argue for past continuity of similar plant communities. *Raillardiopsis muirii* occurs in a variety of Sierran vegetation types, most of the reported associated species having wide distributions. Several perennial species intimately co-occurring with at least one Sierran *R. muirii* population are found on Ventana Double Cone, including *Dudleya cymosa, Eriogonum nudum, E. saxatile, Garrya flavescens, Penstemon breviflorus, Pellaea mucronata, Pinus ponderosa, Polystichum munitum, Potentilla glandulosa, Pteridium aquilinum, Quercus chrysolepsis,* and *Q. kelloggii.* Close Sierran associates found on other high granitic peaks in the Santa Lucia Mountains include *Brickellia californica* and *Pinus lambertiana* (CNDDB 1989; Griffin 1975; Howell 1961). None of these species is as geographically restricted as *R. muirii* (Munz 1959). *Pinus lambertiana* and several additional taxa discussed by Griffin (1975; e.g., *Allium burlewii, A. campanulatum, Carex multicaulis, Chimaphila menziesii, Cornus nuttallii, Ribes roezlii, Sanicula graveolens*) are, however, Santa Lucia Range montane disjuncts that also occur in the southern Sierra Nevada.

Establishment of an *R. muirii* population by long-distance dispersal between the Sierra Nevada and Santa Lucia Range is problematic. The minimum distance between Ventana Double Cone and the closest Sierran population is ca. 240 km. Strong self-incompatibility would have necessitated the eventual establishment of at least two individuals bearing different S-alleles.

Nonetheless, a dramatic example of such dispersal is known in Madiinae. Dispersal between the Sierra Nevada and Santa Lucia Range pales by comparison to the migration event necessary to account for Hawaiian Madiinae (Baldwin 1989). Given the widespread occurrence of self-incompatibility among Hawaiian tarweeds, it appears that the founding colonist(s), in addition to traveling over 3500 km from North America, had to contend with an initial shortage of S-alleles (Carr et al. 1986). This comparison has special relevance for three reasons: (1) chloroplast DNA and biosystematic evidence indicate that *R. muirii* is among the closest extant relatives of Hawaiian Madiinae (Baldwin 1989); (2) propagule characteristics of *R. muirii* are similar to Hawaiian Madiinae species that have undergone repeated inter-island dispersal (e.g., *Dubautia plantaginea*; Carr 1985); and (3) the rhizomatous habit of *R. muirii* would seemingly permit indefinite clonal propagation, allowing persistence of a single self-incompatible colonist while accumulating the S-allele mutations necessary for renewed sexual reproduction, as postulated by Carr et al. (1986) for origin of Hawaiian Madiinae.

Plate tectonics suggests an intriguing hypothesis to explain the Ventana disjunction without long-distance dispersal or wider ecological occurrence of *R. muirii* in prehistoric time. Earliest exposure of granitics in the Gabilan and northern Santa Lucia Ranges after the Miocene could have occurred as long as five million years ago (Stephan A. Graham, Stanford Univ., oral comm.). The Santa Lucia Range was then ca. 240 km southeasterly, based on 48 mm of average annual northwesterly slip of the Salinian Block along the San Andreas Fault (Fig. 3; DeMets et al. 1987). This placed the Tehachapi/San Emigdio granitics, continuous with those of the southern Sierra Nevada, in juxtaposition with the Gabilan Range. The extensive Gabilan granitics are today only 15 km from Santa Lucia exposures nearly continuous with those of Ventana Double Cone (Jennings and Strand 1958). Uplift estimates (Huber 1981) suggest that Sierran granitic exposure was extensive by late Miocene. A wider early Pliocene distribution of *R. muirii* along the southern Sierran Batholith into the San Emigdio region is therefore conceivable. Any populations then extending onto Gabilan or Santa Lucian granitics could have been transported in situ 240 km northwesterly by tectonic slippage along the San Andreas Fault.

Such displacement of *R. muirii* would require that this species is at least five million years old. Though no fossil evidence of Madiinae has been reported, extant tarweed genera are thought by Raven and Axelrod (1978) to have occurred within California by the Pliocene. Accordingly, DNA phylogenetic evidence demonstrated divergence of *R. muirii* and *R. scabrida* prior to the origin of Hawaiian Madiinae (Baldwin 1989). Hawaiian Madiinae appear to be of Kauaian or pre-Kauaian origin (Carr et al. 1989). *Raillardiopsis muirii* is, therefore, conceivably greater than six million years old.

In conclusion, geological and biological considerations reveal that the distribution of *R. muirii* is far from inexplicable. Multiple tenable hypotheses could explain the natural occurrence of *R. muirii* on Ventana Double Cone. Considerable chloroplast DNA differentiation between this population and one from the Sierra Nevada (Baldwin 1989) offers hope for further biogeographic clarification within this species.

## ACKNOWLEDGMENTS

We thank D. Axelrod, G. Carr, J. Griffin, A. Juncosa, D. Keil, J. Shevock, and J. Strother for helpful reviews and discussion; S. Bainbridge and B. Cassidy for field assistance; R. Palmer for *Raillardiopsis scabrida* from Shasta County; G. Carr for cytological assistance; and the curators of the cited herbaria for loans or access to specimens.

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(Received 6 Dec 1988; revision accepted 14 Nov 1989.)

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## ANNOUNCEMENT

### SOUTHWESTERN BOTANICAL SYSTEMATICS SYMPOSIUM

The Sixth Annual Southwestern Botanical Systematics Symposium will be held May 25–26. This year's topic will be "Disjunctions and Their Significance." Invited speakers include: Mary T. Kalin Arroyo, Univ. of Chile; Daniel J. Crawford, Ohio State Univ.; Hong De-Yuan, Academica Sinica, People's Republic of China; David F. Murray, Univ. of Alaska; Clifford R. Parks and Margaret Hoey, Univ. of North Carolina; and Kenneth J. Sytsma, Univ. of Wisconsin. The evening address will be given by Charles B. Heiser, Jr., Univ. of Indiana. The cost is $40.00 ($30.00 for students), and includes Friday evening social, box lunch, and Saturday dinner. To register, send your name, address, and phone number, with a check payable to: Rancho Santa Ana Botanic Garden, Systematics Symposium, 1500 N. College Avenue, Claremont, California 91711. For more information, call (714) 625-8767.